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Empirical Models of Annual Production and P/B Rate for Running Water Benthic Invertebrates

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Published data on secondary production of running water invertebrates are analyzed by multiple regression to quantify the relationship between productivity (*P*, in grams dry mass per square metre per year) and biomass (*B*, in grams dry mass per square metre), mean individual mass (*M*, in grams dry mass), and annual mean water temperature (*T*, in degrees Celsius) to compare productivity of major taxonomic groups and to compare to invertebrate populations from other aquatic ecosystems. The equation $P = 0.18\ B^{1.01}\ M^{-0.34}\ 10^{0.037T}$ explains 87% of the variability in log *P* in the 291 lotic invertebrate populations analyzed. Significant differences were detected among major taxonomic groups, but these differences account for only about 4% of the variability in log *P*. Once the

effect of biomass, mean individual mass and water temperature are taken into account, productivity of lake and stream invertebrate populations is quite similar, although productivity is a linear function of biomass in streams and not in lakes. Comparison of models for running waters, lake and marine ecosystems suggests that marine invertebrates are less productive than freshwater populations.

Des données publiées sur la productivité d'invertébrés d'eau courante sont réanalysées par régression multiple afin de (1) quantifier la relation existant entre la productivité (*P*, en grammes de masse sèche par mètre carré par an), la biomasse (*B*, en grammes de masse sèche par mètre carré) la masse individuelle (*M*, en grammes de masse sèche) et la température moyenne annuelle de l'eau (*T*, en degrés Celsius), (2) de comparer la productivité des principaux groupes taxonomiques et (3) de comparer cette relation à celles observées pour de populations d'invertébrés d'autre écosystèmes aquatiques. La relation $P = 0.18\ B^{1.01}\ M^{0.34}\ 10^{0.037T}$ explique 87% de la variabilité de log *P* entre les 291 populations d'invertébrées lotiques analysées. Des différences significatives ont été détectées entre les principaux groupes taxonomiques, mais ces différences n'expliquent qu'environ 4% de la variabilité de log *P*. La

productivité des invertébrés de lacs et d'eau courante est très similaire lorsque corrigée pour l'effet de la biomasse, la masse individuelle et de la température. Contrairement à ce qui a été observé pour les lacs, la productivité est reliée linéairement à la biomasse pour les invertébrés vivant en ruisseaux et rivières. La comparaison de la relation pour les écosystèmes d'eau courante, de lac et marin suggère que les populations d'invertébrés marins sont moins productives que les populations dulcicoles.

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The rational use of natural renewable resources presupposes knowledge of the factors affecting their production. Besides affecting the recycling and retention of nutritive elements, invertebrates in lotic ecosystems influence the energy transfer from prime producers and allochthonous material towards fish. Thus their production is an important aspect to consider in the development of streams and rivers and their use for recreational purposes.

Studying population production is, however, a complex and costly undertaking, involving as it does rigid sampling and estimation of several demographic parameters. (Benke 1984; Rigler and Downing 1984). Ways of avoiding these logistical problems have

been suggested by several researchers. Because of the apparent relationship between the production/biomass rate (P/B) and life cycle characteristics, Mann (1969) and Waters (1977) have suggested using the product of the annual mean biomass and the P/B rate presumed as a function of the life cycle to give a rough estimate of production. This approach was developed by Banse and Mosher (1980), who demonstrated an empirical relationship between the P/B rate and individual mass at maturity for several groups of organisms.

More recently, Plante and Downing (1989) developed an empirical model linking the annual production of lake benthic and planktonic invertebrates to their biomass, their maximal individual weight and the annual mean temperature. Brey (1990) followed a similar approach by linking production of marine and lake benthic macroinvertebrates to annual mean biomass and mean individual mass. Plante and Downing (1989) did not analyze data on running water invertebrates because of the radical differences between lotic and lentic environments. Brey (1990) did not include data on insects in his analysis because of the unique life cycle of benthic macroinvertebrates. The effect of temperature was not analyzed by Brey. Thus there is no empirical model linking lotic insect production to biomass, individual mass and temperature. Moreover, if we accept the arguments of Plante and Downing (1989) and Brey (1990), the published models should not be used for these organisms.

We present here an analysis of the published data in an attempt to quantify the relationship between lotic macroinvertebrate production on the one hand and annual mean biomass, annual mean mass and annual mean temperature on the other. The purpose of this analysis is to produce a general equation that will allow us to estimate lotic invertebrate production and to compare the production of various taxonomic groups, in order to determine whether it is better to use several specific equations rather than one general equation. The relationship between production, biomass, mean weight and temperature for running water invertebrates is subsequently compared with the relationships described by Brey (1990) and Plante and Downing (1989) to determine whether there are differences in production and P/B rate among benthic invertebrates found in streams and rivers and those found in lake and marine ecosystems.

Methods

Data selection

Data on secondary production (P, in grams dry mass (DM) per square metre per year), annual mean biomass (B, in grams DM per square metre) and mean individual mass (M, in grams DM) were chosen from literature published between 1979 and 1990 in *Aquatic Insects, Canadian Journal of Fisheries and Aquatic Sciences, Canadian Journal of Zoology, Ecological Monograph, Ecology, Freshwater Biology, Holarctic Ecology, Hydrobiologia, Journal of the North American Benthological Society and Limnology and Oceanography*. Only

estimates based on a sampling for the whole year and accompanied by water temperature data (T, in degrees Celsius) were retained. Production estimates obtained by multiplying the mean biomass by the P/B rate for another population were also rejected. When necessary, data expressed in wet mass or dry mass units without ash were were converted into dry mass units by using the conversion factors of the authors or those of Hamill (1975). Mean individual mass was calculated by dividing the annual mean biomass by the annual mean density. Data on production, biomass and dry mass for Mollusks do not include shell. The annual mean water temperature, when not given in the articles, was calculated from data in tables and figures by using the mean of the given temperatures, weighted by the time interval corresponding to each reading.

Statistical analyses

The relationship between production and biomass, mean individual mass and water temperature was first quantified from the body of data by estimating the coefficients of a multiple linear regression model in the form

(1) $\log_{10}P = a + b \log_{10}B + c \log_{10}M + dT.$

The logarithmic transformation of P, B and M linearizes the relationship between these variables and stabilizes the variance of residual error.

Subsequently, analysis by multiple regression was repeated separately for each of the main taxonomic groups. The regressions for each group were compared through analysis of covariance

(ANCOVA) to determine whether the coefficients (a, b, c and d in Eq. 1) vary significantly from one group to another. The regressions for each group were also compared individually to the estimated regression for the entire body of data to determine whether the general model can be applied to particular groups without the predicted values being significantly biased. These comparisons were done by means of an F test (with 4 degrees of freedom for the numerator and n - 4 degrees of freedom for the denominator) in the relationship

(2) $$F = \frac{(SC_{Taxon} - SC_{General})}{4s^2_{Taxon}}$$

where N is the number of observations for the taxonomic group for which the regression equation is compared to the general equation; SC_{Taxon} and $SC_{General}$ are respectively the sum of the squares of the deviations attributable to the specific regression and the general regression when applied only to the data of the taxonomic group being compared, and s^2_{Taxon} is the variance of residual error of the regression for the taxon being compared.

Results

Description of the data

The analyses are based on 291 production estimates from 35 published studies on the populations of 32 streams and rivers, found mainly in the temperate regions of the northern hemisphere (Table 1). The majority (272/291) of the annual production estimates were calculated by the size frequency method (Hynes-

Hamilton; Benke 1984; Rigler and Downing 1984). Table 2 gives a summary of the values observed.

General model

Analysis by multiple regression of the data shows that the production of running water invertebrates is positively linked to both their biomass and the water temperature and negatively linked to mean individual mass. The regression equation

(3) $\log P = -0.75 + 1.01 \log B - 0.34 \log M + 0.037 T$

$n=291;\ R^2 = 0.87;\ RMS = 0.117$

explains 87% of the variability observed between the values for log P (Fig. 1). Of the three independent variables, the annual mean biomass is the most closely linked to production (partial correlation of 0.93; $p < 0.0001$), and it alone explains nearly 79% of the variability of log P. The mean individual mass (partial correlation of -0.63; $p < 0.0001$) and the temperature partial correlation of 0.47; $p < 0.0001$) explain respectively 8.6 and 3.8 % of the variability of log P in this set of data. The values observed vary on the average by a factor of 2.2 from the predicted values, but in the worst cases they can differ from the predicted values by a factor of 10.

Comparison of taxonomic groups

The comparison of the observed production and that predicted by the general model (Fig. 2) illustrates the strong correlations between observed and predicted values. It suggests, however, that

there are differences in production among certain taxa that cannot be explained by differences in biomass, mean mass or water temperature. On the average, the general model underestimates production of Diptera (mean of residual errors (RMS) = 0.09; t,p test = 0.017) and Megaloptera (mean = 0.30; $p = 0.018$); and it overestimates production of Mollusca (mean = 0.76; $p < 0.0001$) and Coleoptera (average = 0.45; $p = 0.0014$).

TABLE 1. List of sites for which production data was retained. The number of production estimates (n) and the mean annual water temperature are given for each site.

Site	Coordinates	n	Temperature (°C)	Reference(s)
Anna River	37°N, 77°W	1	18.4	Parker and Voshell 1983
Ball Creek	35°N, 83°W	43	8.3	Huryn and Wallace 1985, 1987a, 1987b, 1988
Black Creek	32°N, 83°W	1	19.5	Benke and Parsons 1990
Blanco	29°N, 98°W	1	21.9	Short et al. 1987
Buzzard	37°N, 76°W	19	16.0	Roeding and Smock 1989
Cedar Creek	33°N, 81°W	32	17.6	Smock et al. 1985
Dryman Fork	36°N, 86°W	24	9.5	Ross and Wallace 1983
Fonstrup Back	58°N, 12°E	1	9.1	Iversen 1980
Grabia River	52°N, 19°W	14	9.0	Grzybkowska and Witczak 1990
Guadelupe	29°N, 98°W	1	20.5	Short et al. 1987

Hidden	43°S, 170°E	1	10.0	Collier and Winterbourn 1990
Honey	29°N, 98°W	1	21.4	Short et al. 1987
L'Achigan	46°N, 74°W	2	8.4	Lauzon and Harper 1986
Little Shultz	33°N, 87°W	2	17.3	Richardson et al. 1988
Moat Feeder	51°N, 3°W	1	10.1	Lazim and Learner 1986
Ogeechee	32°N, 83°W	2	19.3	Benke and Parsons 1990
Ottawa River	46°N, 73°W	23	9.0	Hamill et al. 1979
Palau	7°N, 134°E	9	25.5	Bright 1982
River Ely	51°N, 3°W	1	11.8	Murphy and Learner 1982
Rold Kilde	56°N, 9°E	2	7.5	Iversen and Jessen 1977
Rose Creek	33°N, 83°W	2	17.5	Freeman and Wallace 1984
Samson	49°N, 4°E	4	9.4	Rosillon 1986
San Marcos	29°N, 98°W	1	22.2	Short et al. 1987
Satilla	31°N, 82°W	52	19.0	Benke et al. 1984
Savannah	32°N, 81°W	17	16.5	Cudney and Wallace 1980
Steep	43°S, 170°E	1	9.5	Collier and Winterbourn 1990
Suspect	43°S, 170°E	1	10.5	Collier and Winterbourn 1990
Sycamore	33°N, 110°W	7	18.5	Jackson and Fisher 1986
Tallulah	34°N, 83°W	6	11.0	Benke and Wallace 1980
Toilet	43°S, 170°E	1	11.0	Collier and Winterbourn 1990

Valley Creek	45°N, 92°W	18	9.1	Waters and Hokenstrom 1980; Mackay and Waters 1986.
Valley River	51°N, 100°W	1	10.0	Giberson and Galloway 1985

TABLE 2. Minima, maxima and medians of values of biomass, mean individual mass, water temperature and production.

Variable	Units	Minimum	Maximum	Median
Biomass	g $DM.m^{-2}$	0.0006	45.7	0.041
Individual mass	mg DM	0.0008	186	0.35
Temperature	^0C	7	25.5	16
Production	g $DM.m^{-2}.yr^{-1}$	0.003	138	0.4

The relationship between production and biomass, mean mass and temperature varies among taxa (Table 3). Regression coefficients associated with biomass, individual mass and temperature vary significantly among the main taxonomic groups (ANCOVA; F - 6.45; 27 dl, 259 dl; P<0.0001). The differences in slope and ordinates at the origin among the groups explains about 30% of residual variability of the general model, which equals about 4% of the total variability of log P. However, a precise estimate of the

coefficients of the models for these taxa could not be made because of the low numbers in most groups.

Not only do the regressions for the different taxa differ among each other, but several differ significantly from the regression on the complete body of data: regressions for Coleoptera ($F = 526$; 4dl, 1 dl; $P = 0.03$), Diptera ($F = 2.7$; 4 dl, 66 dl; $P = 0.04$), Odonata ($F = 16.5$; 4 dl, 6 dl; $p = 0.002$), Plecoptera ($F = 5.9$; 4 dl, 9dl; $p = 0.01$) and Trichoptera ($F = 7.6$; 4 dl, 104 dl; $p < 0.0001$).

The precision of the values predicted by the regression equations varies significantly among the main taxonomic groups. As suggested by the dispersion of the observed values in relation to the predicted values in Fig. 2, the variance of residual error of the regressions for the Diptera (0.196) and Ephemeroptera (0.147) is clearly higher than those observed for other groups. A Kruskal-Wallis test performed on the absolute values of the residual errors of the 10 models shown in Table 3 showed a significant difference in precision between the taxa (chi-squared = 74; 9 dl; $p < 0.0001$).

Discussion

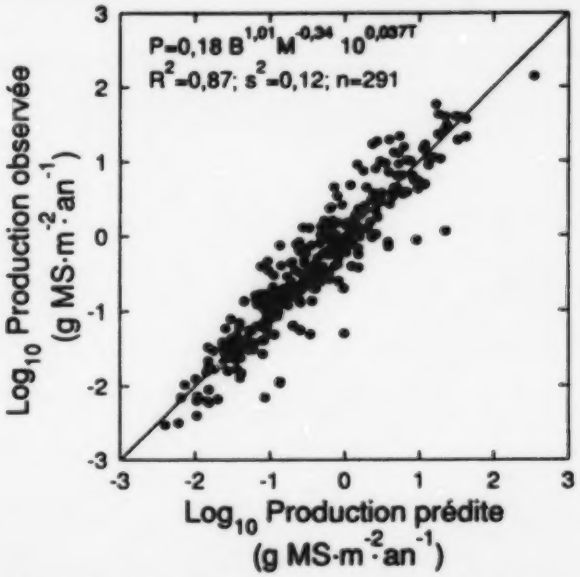
Biomass

The production of lotic invertebrates is directly proportional to their mean annual biomass. The coefficient associated with the biomass in the general model (1.01) does not differ significantly from 1.0, which implies that the production of invertebrates is linearly related to their biomass and that the P/B rate is not

influenced by the biomass. This result is identical to that of Brey (1990), who also obtained a coefficient

$P=0.18\ B^{1.01}M^{-0.34}100.037T$

$R^2=0.87;\ s^2=0.12;\ n=291$



Log_{10} Observed Production ($g\ DM.m^{-2}.year^{-1}$)

Log_{10} Predicted Production ($gDM.m^{-2}.year^{-1}$)

Fig.1 Production observed and predicted by the general model for lotic invertebrates (Eq. 3). The diagonal is line 1.1.

of 1.01 for the biomass of marine and lake benthic invertebrates. Banse and Mosher (1980) noted the absence of a relationship between the P/B rate and the mean biomass, which also implies that production is directly proportional to the biomass. Humphreys (1981), in his analysis, noted that the coefficient linking production (log P) to an index of the density of populations corrected for their metabolic capacity (log I_m, i_m being calculated in the same manner as $BM^{-0.75}$) was 0.68 for terrestial and aquatic invertebrates, which implies that production is proportional to $B^{0.68}$. An analysis of multiple regression of the Humphries (1981)

data gives, after unit conversion (1 kcal ≈ 0.2 g DM; 1 g wet mass ≈ 0.2 g DM):

(4) $\log P = -0.12 + 1.15 \log B - 0.25 \log M'$

$n = 32$; $R^2 = 0.83$; RMS = 0.192

where M′ is the maximal dry mass (grams DM) and or the coefficient for the biomass does not differ significantly from 1.0. Plante and Downing (1989), however, observed a significantly lower value (0.79) for lake invertebrates, which implies a non-linear relationship between production or P/B rate and biomass. The relationship between production and biomass seems, therefore, to be different for lake invertebrates.

Individual mass

For a given biomass and temperature, lotic invertebrate production declines when size increases ($P \alpha M^{-0.34}$). The coefficient for individual mass (CI 95%: -0.38 to -0.30) is significantly lower than the theoretical value of -0.25 commonly observed for specific metabolic rates (Peters 1983). When the error associated with the coefficients of regression is, however, taken into account, the observed value does not differ significantly from the coefficients estimated by Banse and Mosher (-0.34 for mean adult mass, CI 95%: -0.41 to -0.28) and Brey (-0.27, CI 95%: -0.31 to 0.24), nor from the value of -0.25 (maximal DM, CI 95%: -0.37 to -0.13) recalculated from the Humphreys data. On the other hand, our results contradict Plante and Downing's (1989) generalization based on their analysis of the relationship

between production and maximum individual mass (M_{max} in DM milligrams, exponent = -0.16) whereby the exponent associated with individual mass is greater than -0.25 for aquatic invertebrates.

The use of M_{max} instead of M in Plante and Downing's (1989) regression model for lake invertebrates appears to explain the exponential difference in individual mass between lakes and streams. Analysis of a subset of the Plante and Downing data (1989) for which we were able to obtain the mean individual mass shows that production of lake invertebrates can be described by the relationships

(5) $\log P = 0.24 + 0.82 \log B - 0.17 \log M_{max} + 0.044 T$

$n = 53$; $R^2 = 0.70$; RMS = 0.173

(6) $\log P = -1.25 + 0.85 \log B - 0.34 \log M + 0.059 T$

$n = 53$; $R^2 = 0.77$; RMS = 0.135.

The use of M instead of M_{max} in the multiple regression on this subset of data explains the 7 % higher variability in log P and lowers the coefficient associated with individual mass (CI 95%: -0.46 to 0.26) to the value observed for lotic invertebrates.

Temperature

Equation 3 shows that production increases with temperature and is proportional to $10^{0.037T}$, which gives a Q_{10} of about 2.3. The effect of temperature on production is higher than that observed for specific growth rates for simulid larva (Q_{10} = 1.4; Morin et al. 1988b), but similar to that observed for their ingestion rate (Q_{10} = 2.2; Morin et al. 1988a). Plante and Downing (1989) report a

much more significant effect of temperature (Q_{10} = 3.2) on the production of lake invertebrates.

P/B rate

Equation 3 enables us to calculate expected P/B rates as a function of mean individual mass and water temperature (Fig. 3). The P/B rate increases when temperature increases and decreases when mean individual mass increases. The high P/B rates for small warm-water organisms described in Fig. 3 concur rather well with values observed by Benke and Parsons (1990) for simulids in rivers in the southeastern United States (37-85).

Comparison of taxonomic groups

Like Brey (1990), we noted differences in production among taxa that cannot be explained by biomass, individual mass or temperature. By comparing models estimated for the main taxonomic groups, we were able to detect relatively small but statistically significant differences; these differences between groups explain only about 4 % of the total variability of log P, as compared with the 87 % explained by the general relationship. By using specific models we can thus predict production somewhat more precisely than by using a single equation for all groups, and, above all, we eliminate the bias of the general model for certain groups.

Log_{10} Predicted Production

(g $MS.m^{-2}.an^{-1}$)

Amphipoda

Isopoda

Diptera

Trichoptera

Ephemeroptera

Plecoptera

Odonata

Megaloptera

Mollusca

Coleoptera

Oligochaeta

Log_{10} Predicted Production

(g $MS.m^{-2}.an^{-1}$)

FIG. 2. Observed production for different taxa as a function of production predicted by the general model (Eq. 3). SEE PAGE 17a.

It is possible, however, that the differences noted reflect differences between studies or sites rather than fundamental differences between taxonomical groups. Since the body of data was drawn from only a limited number of studies and the data for the different taxonomical groups do not typically come from the same sites, it is possible that the differences noted between groups are due to factors other than biomass, individual mass, temperature or taxa. Supplementary data, ideally collected under similar

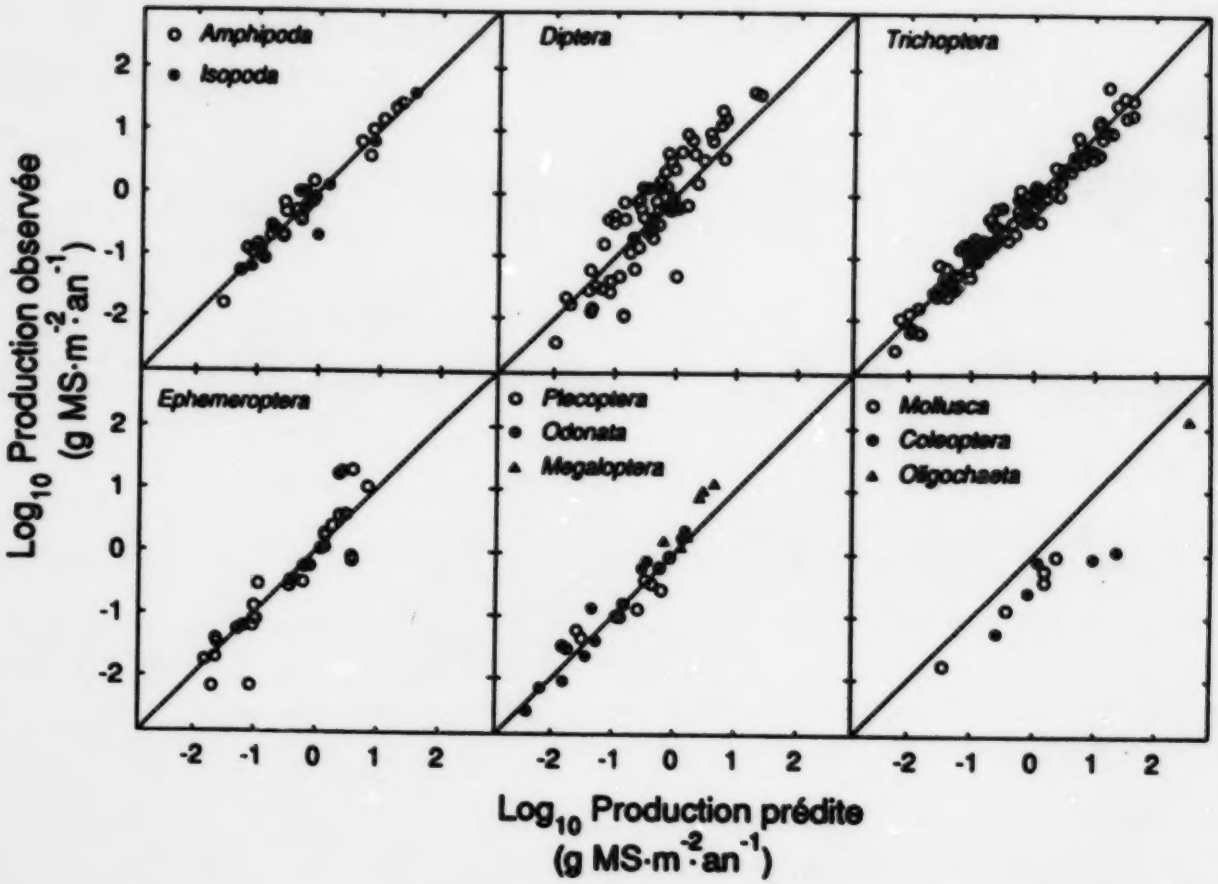


Fig. 2 Observed production for different taxa as a function of production predicted by the general model (Eq. 3) -- See page 17.

conditions from the same sites, would enable us to establish the reason for the differences observed between groups.

In any case, our results do not support Brey's (1990) reservations regarding the effect of the differences in the life cycle on production. We have not observed strong differences in production (corrected for B, M and T) between crustaceans and insects. For lack of more precise, specific models, Equation 3 can be used for all groups of lotic invertebrates.

Comparison between aquatic ecosystems

Contrary to the beliefs of Plante and Downing (1989), production of organisms in lakes and running water seems little affected by the strong differences in the physical conditions of these ecosystems. Production of lake invertebrates (benthic and planktonic) can, on the average, be adequately predicted by using Eq. 3 (Fig. 4) but by underestimating lower production levels and overestimating the higher ones. Comparison of Equations 3 and 6 suggests that it is mainly the relationship between P and B that varies in these habitats. The difference could also be explained by a difference between estimates used for the lake model and those used for running water. The data used here were almost all obtained by the size frequency method (Hynes-Hamilton), whereas those used for the lake model were mainly obtained by other methods which were considered to be more precise (Morin et al. 1987). Plante and Downing (1990), however, were not able to detect any bias from the various methods for estimating production in their analysis of the

residual variability surrounding the values predicted by their model for lakes. Thus, it is rather unlikely that the slight differences noted between lake and running water ecosystems could be due to a difference in the methods used.

On the other hand, Brey's (1990) model, which was estimated mainly from data on marine invertebrates, implies that the P/B rate for these organisms is typically lower than that observed for freshwater invertebrates. The differences noted for fresh and salt water habitats could be due to the differences in the taxonomic groups studied by Brey (his data is dominated by mollusks), or partly because of a difference in temperature.

Table 3. Multiple regression models estimated for the main taxonomic groups. Coefficients (and standard error, SE) of the multiple regression error between the logarithm of production (g $DM.m^{-2}.yr^{-1}$) and the logarithm for the annual mean biomass (log B, g $DM.m^{-2}$), the logarithm for mean individual mass (log M, g DM) and the annual mean water temperature (T, ^{o}C). The number of observations (n), the coefficient of multiple determination (R^2) and the variance of residual error (RMS) are also given for each regression. The asterisks indicate the probability that the coefficient of partial regression equals zero (t test: ^{ns} $p > .05$, $*0.05 > p > 0.01$, $**0.01 > p > 0.001$; $***p < 0.001$).

Model	*n*	Intercept (SE)	log *B* (SE)	log *M* (SE)	*T* (SE)	R^2	RMS
General	291	-0.75	1.01***	-0.34***	0.037***	0.87	0.117
		(0.09)	(0.02)	(0.02)	(0.004)		
Amphipoda	31	0.60	1.02***	0.02^{ns}	0.016^{ns}	0.96	0.025
		(0.53)	(0.04)	(0.16)	(0.018)		
Coleoptera	5	1.80	0.94*	0.24^{ns}	-0.015^{ns}	0.99	0.001
		(0.60)	(0.02)	(0.08)	(0.018)		
Diptera	67	-1.07	1.12***	-0.38***	0.062***	0.79	0.196
		(0.37)	(0.09)	(0.08)	(0.014)		
Ephemeroptera	35	-0.26	1.11***	-0.25^{ns}	0.035*	0.85	0.147
		(0.50)	(0.09)	(0.13)	(0.013)		
Isopoda	6	-0.43	1.05*	-0.29^{ns}	0.017^{ns}	0.98	0.080
		(0.42)	(0.13)	(0.14)	(0.020)		
Megaloptera	6	-3.90	1.15	-0.44^{ns}	0.198^{ns}	0.95	0.020
		(8.40)	(0.34)	(1.21)	(0.313)		
Mollusca	5	3.90	-0.40^{ns}	0.89^{ns}	-0.120^{ns}	0.91	0.105
		(4.41)	(0.88)	(0.85)	(0.143)		
Odonata	10	-0.01	0.97***	-0.01^{ns}	0.035**	0.99	0.008
		(0.21)	(0.04)	(0.06)	(0.009)		
Plecoptera	13	-0.62	0.69***	-0.16*	0.033**	0.94	0.018
		(0.30)	(0.07)	(0.06)	(0.010)		
Trichoptera	108	-0.18	1.00***	-0.19***	0.027***	0.96	0.035
		(0.12)	(0.02)	(0.03)	(0.004)		

Temperature (°C)

Body Mass (mg DM)

Fig. 3. P/B rate for running water invertebrates as a function of water temperature and mean individual mass. Values are calculated by using Equation 3. (See p. 21a)

Log_{10} Observed production
(g $DM.m^{-2}.yr^{-1}$)

Log_{10} Predicted production
(g $DM.m^{-2}.yr^{-1}$)

Fig.4. Comparison of production in lakes and running water. Observed production for Downing and Plante's (1989) subset of data on lake invertebrates for which we were able to estimate the mean individual mass as a function of the predicted production using the general model for running water (Eq. 3). The short line is the line of regression log $P_{observed}$ = 0.06 + 0.831log $P_{predicted}$ (n = 53). The slope of this line is significantly less than 1.0 (p = 0.013). (See p. 21a)

P/B Rate ($year^{-1}$)

lake (1 $mgDM.m^{-2}$)

Brey (1990)

stream

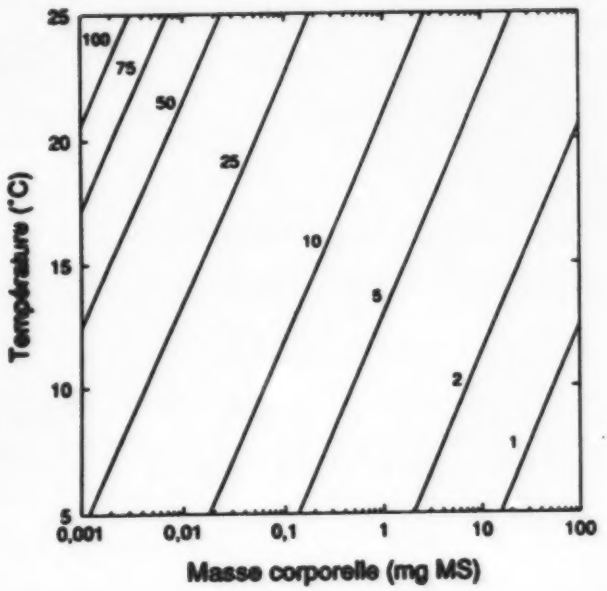


Fig. 3 (see p. 21)

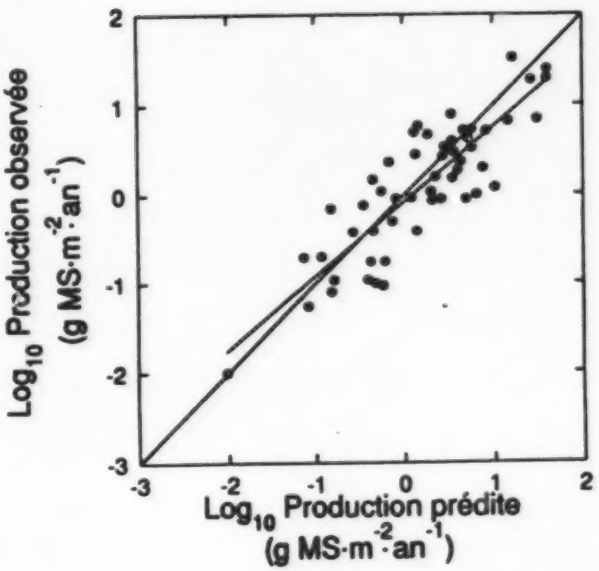


Fig. 4 (see p. 21)

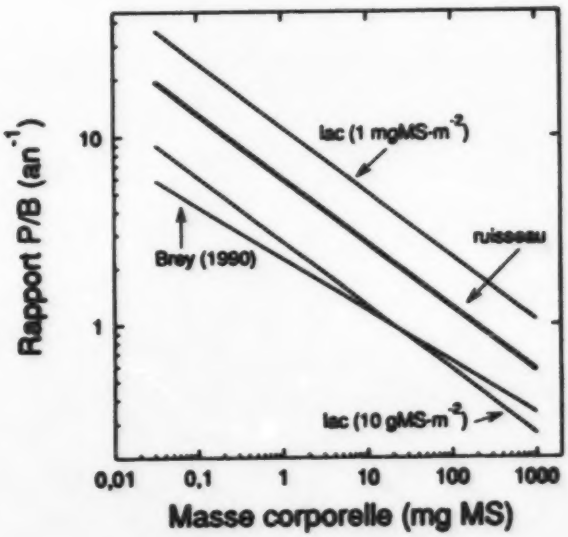


Fig. 5 (see p. 22)

lake (10 $gDM.m^{-2}$)

Body Mass (mg DM)

Fig. 5. Relationship between the P/B rate and mean individual mass for lakes, streams and the Brey (1990) data, which includes mostly marine invertebrates. The lines for streams and lakes were calculated from Eq. 3 and 6 respectively, for a temperature of 14°C. As the P/B rate is influenced by the lake biomass, the relationship shown is for a low biomass (1 $mgDM.m^{-2}$) and for a high biomass (10 g $DM.m^{-2}$). (See p. 21a)

The P/B values for lakes and streams illustrated in Fig. 5 were calculated for a temperature of 14 °C, which corresponds to the mean value of the Plante and Downing (1989) data and those analyzed here. If Q_{10} is 2.0, the difference in the P/B rate for streams and the Brey data is about 15°C. The annual mean temperature for the sites from which this data was gathered would have to be about 0 °C to bring the line to the level of the one for running water. Since the greater part of the Brey data comes from the coastal zone in temperate regions, it is rather unlikely that the difference is due entirely to a difference in temperature. A more thorough analysis, which would include the effect of temperature, would nonetheless be desirable to determine whether marine organisms are really less productive than freshwater organisms.

Precision of estimates and possible improvements

The adjustment of the observed values to the regression equations of the same type as Eq. 3 is very good, considering the errors in the biomass measurement and the production of natural populations (Morin et al. 1987). The precision of the empirical models could no doubt be improved. Plante and Downing (1989) identified several variables that can explain a significant fraction of the residual variability for the model they show for lakes. Most of these variables can be considered as indices for primary production. A large part of the remaining variability for lotic invertebrates can no doubt be explained by the availability of food. The gain in precision should, however, be compared with the cost of measuring supplementary variables.

A slightly different temperature index from the one used here could perhaps improve the precision of the predictions without increasing the cost of measurement. Benke and Parsons (1990) mention that the annual P/B rate for simulid populations varies substantially between sites with similar annual mean temperatures. He explains this difference by the fact that the populations do not reach their maximal biomass at the same time during the year, which means that the most productive periods of these populations occur at different temperatures. This type of situation cannot be accommodated by using the annual mean temperature as an index for the temperature to which the productive biomass was exposed on the average. On the other hand, if the annual mean temperature is

weighted by the biomass to create an index of the temperature T', calculated, for example as

$$(7)\quad T' = \frac{\sum_{i=1}^{n} B_i T_i}{\sum_{i=1}^{n} B_i}$$

where B and T are the biomass and the temperature observed for each sampling date is i, then this index would take into account the phenology of the production. Such an index could enable us to make precise predictions on production in situations such as those described by Benke and Parsons and in cases where models of the same type as Eq. 3 would be inadequate.

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